SCIENCE

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*PALEONTOLOGY AS A MORPHOLOGICAL DISCIPLINE.**

THE day has forever gone by when any one mind, however profound and comprehensive, can take all knowledge for its province. Increase of knowledge, like advance of civilization, necessarily brings with it a division of labor, and each of the great branches of science becomes more and more minutely divided and subdivided for the purposes of investigation. Such subdivision greatly enhances the efficiency of the individual worker, enabling him to concentrate his attention upon some definite problem of more or less limited scope, and, so far, it is advantageous. On the other hand, like most human devices, it has its drawbacks, and what is gained in one direction is apt to be lost in another. One great and growing evil is the subdivision of *knowledge* which accompanies specialization of research. The worker finds the greatest difficulty in keeping abreast of all that is being accomplished by fellow laborers in his own field; how, then, shall he find time to learn anything of the work in other fields? Not to do so involves the penalty of such a narrowness of view as will inevitably lessen the value of his own work, because deductions drawn legitimately enough from a single line of investigation often appear absurd when tested by a wider range of facts. Many a blunder might be avoided, were the worker's vision not so strictly limited by the boundaries of his own speciality.

The narrowing effects of this subdivision of knowledge result in a more or less marked loss of sympathy and mutual understanding between the representatives of the different branches of the same science. To

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magnify one's own office is a very human infirmity, but it involves a minimizing of the offices of others. Science is not advanced by the sneers of its representatives at one another as mere 'species-makers,' or 'section-cutters,' or 'closet-naturalists,' as the case may be. One is prone to regard with instinctive distrust results which run counter to cherished convictions, or which ill harmonize with prevalent theories and call for a radical readjustment of opinion. Naturally the investigator is apt to place undue reliance upon the methods with which he is familiar and to undervalue other ways of attacking the same problem. Evidence derived from other lines of investigation means less to him and is the more readily overlooked and ignored. Perhaps the greatest danger which at present threatens the healthy growth of zoological science in all its branches is the ever-increasing tendency to ambitious speculation, founded upon the narrowest basis of fact. So much of a theoretical taint attaches to nearly all morphological work as to cause hesitation in fully accepting it, and one often feels in reading that we have gone back to the days of the transcendental anatomists. The glib use of phrases and formulæ, which hide ignorance under the guise of 'explanations' which do not explain, is an outgrowth of the same tendency. It is the fashion to measure with elastic standards, which expand and contract to meet the needs of each case. Dogmatism and narrow-mindedness have ever been closely akin.

The obvious corrective for many of these evils is to take a wider view of our subject, and for each of us to learn something of the methods and results of workers in other fields than our own. I wish to invite your attention to a branch of morphology, the bearings of which are much misapprehended by the representatives of other departments of the same science, and which, where not completely ignored, is often wofully abused, namely, the subject of paleontology. This science has too long been abandoned to the geologist, but morphologists are coming to see that they have an interest in it, and sometimes condescend to make use of such parts of its data as favor their opinions. Even yet, however, the necessary and close connection which obtains between paleontology and geology leads many to the assumption that its relation to morphology is, at best, very remote; but this assumption is quite unjustified, and proceeds from a confounding of the two quite distinct aspects and offices of paleontology. One of these offices is to determine the chronological succession of the rocks, and in this morphology is very indirectly concerned; but the other office is the study of fossils as organisms, and here Huxley's dictum thoroughly applies: "The only difference between a collection of fossils and one of recent animals is that one set has been dead somewhat longer than the other." This is a shining example of the 'true word spoken in jest.'

The great problems of morphology are the same for all workers in that science; it is the method of attacking them which differs. If I may be allowed to quote what I have elsewhere said, I would again call attention to the very instructive character of the analogies which exist between the history, aims and methods of animal morphology and those of comparative philology. "In both sciences the attempt is made to trace the development of the modern from the ancient, to demonstrate the common origin of things now widely separated and differing in all apparent characteristics, and to establish the modes in which, and the factors or causes by which, this evolution and differentiation have been affected. At the present time morphology is still far behind the science of language with regard to the solution of many of these kindred problems,

and can hardly be said to have advanced beyond the stage which called forth Voltaire's famous sneer: 'L'étymologie est une science où les voyelles ne font rien et les consonnes fort peu de chose.' Of the animal pedigrees, now so frequently propounded, few have any better foundation than the guessing etymologies of the last century, and for exactly the same reason. Just as the old etymologists had no test to distinguish a true derivation from a false one, except a likeness in sound and meaning in the words compared, so the modern morphologist is yet without any sure test of the relationships of animals, except certain likenesses or unlikeness of structure. How much weight is to be allowed a given similarity, and how far this is offset by a dissimilarity which accompanies it, we have, as yet, few means of determining, and have still to discover those laws of organic change which shall render the same service to morphology as Grimm's law has done to the study of the Aryan tongues."

Philology was raised to the dignity of a true science by the laborious tracing back of modern words, step by step, to their ancient origins, through all their intermediate gradations, and sound principles of etymology could not be established until this was done. Morphology must profit by this lesson and must imitate the method of the science of language. Not until many long phylogenetic series have been recovered, can the law of change be worked out. It is just here that paleontology is fitted to render invaluable services to the common cause.

As every one is aware, the principal methods of morphological inquiry are comparative anatomy, embryology and paleontology, each of which has its great advantages, but accompanied by its own peculiar drawbacks and limitations. Lack of time will prevent any discussion of Bateson's proposed new method for the study of variation. I have elsewhere examined that at some length.

The foundation and corner stone of the whole structure of morphology must ever be comparative anatomy, an accurate knowledge of which is indispensable to successful prosecution of the other departments of inquiry. This method has, in the hands of the masters, registered many great triumphs in the solution of difficult problems of homology and of the mutual relationships of animal groups. At the present time the tendency is to give more and more weight to its determinations. On the other hand, finality cannot be reached by this method. It suffers from the very significant drawback of possessing no sure criterion by which to distinguish between those similarities of structure which result from actual genetic relationship and those which are due to parallel or convergent development, and thus to determine the taxonomic value of a given likeness or unlikeness. It is an exceedingly common fallacy to assume that, because a number of allied groups display a certain structure, their common ancestor must also have possessed it. This may have been the case, but it is almost as likely not to have been, because the structure in question may have been many times independently acquired. While the comparative method frequently enables us to discriminate between the two classes of phenomena, it generally does not do so, and it never can give entire certainty upon this point.

On comparing the humerus of the horses with that of the camels, we find in each a characteristic difference from other artiodactyls and perissodactyls and agreement with each other—a feature which may be described in brief as the duplicity of the bicipital groove and presence of a bicipital tubercle. It is *à priori* probable that such an isolated resemblance between two widely separated groups is due to convergence, and yet the comparative method can give us no

assurance that this is not a primitive ungulate character retained in these two series and lost in the others. Having recovered the various extinct genera of both these phyla, we may trace out the gradual transformation of the humerus and definitely show that the resemblance has been independently acquired at a comparatively late period, and is not a case of a persistent primitive feature.

In short, the difficulty of reaching firmly fixed conclusions upon questions of homology and relationship by the exclusive use of comparative anatomy lies in the fact, that this method deals only with the modern assemblage of animals, a mere fragment of that which has existed in former times. It is like attempting to work out the etymology of a language which has no literature to register its changes.

The second method of morphological inquiry, embryology, has had a somewhat chequered career. Not many years ago it was universally regarded as the infallible test of morphological theory, and the principle that the ontogeny repeated the phylogenetic history in abbreviated form was accepted, almost without question, as a fundamental law. But this view has fallen somewhat into discredit. The admission which very early had to be made, that 'cenogenetic' features of development were imposed upon or substituted for those due to ancestral inheritance, opened the door to an unduly subjective way of dealing with embryological evidence and deprived the method of that authoritative character which had so generally been ascribed to it. Now the whole recapitulation theory is boldly called in question, and, in the admirable lecture delivered last year in this place, Prof. E. B. Wilson showed the untrustworthy nature of the embryological criterion of homology. The difficulty in this case lies in the absence of any 'canons of interpretation' (to use Bateson's phrase) by which the contradictory data of embryology may be harmonized into a consistent whole. To take a concrete illustration: The ontogenetic development of the horse's teeth would give us a very inadequate and indeed false conception of the actual steps of change, by which the modern type of dentition has been attained, nor would embryology show that the horse is descended from five-toed ancestors. Knowing, as we do from the fossils, the phyletic series, the embryological facts may be readily understood. It is an undue reliance upon such facts which has led to the concrescence theory of tooth development, now so rife in Germany and which seems so absurd when viewed in the light of paleontology.

I have no intention of belittling the splendid services which embryology has rendered to morphology, but merely to point out that this method alone cannot reach finality any better than comparative anatomy. It resembles dealing with a literature that has been vitiated by many forgeries, only the grossest and most palpable of which can be readily detected.

A third method of attacking morphological problems is that offered by paleontology. Let us begin our consideration of this method by frankly acknowledging its drawbacks and limitations. (1) In the first place there is the imperfection of the geological record. Paleontology does not profess and never can hope to reconstruct the whole history of life upon the earth, or even the greater part of that history; very many chapters are irretrievably lost, and others are so fragmentary that they teach us little or nothing. The great sedimentary deposits which contain nearly the whole recorded history of the globe were laid down under water, and for a land animal or plant to be entombed there is a lucky accident. If all we could learn of the terrestrial life of North America had to be deciphered from

the fragments enclosed in the oceanic deposits along its shores, how very imperfect would our knowledge be! Although the estuarine, swamp and lake formations, which occur on such a grand scale among the rocks of the earth's crust, have preserved whole chapters in the history of terrestrial life with wonderful fullness and accuracy, they are all too few and too widely separated to form any complete record. Even in a continuous series of marine deposits, representing vast periods of time, there are sure to be gaps of greater or less importance in the record. Changes in the depth of water and the character of the bottom will drive out one set of forms from that locality and bring in another, which has no genetic connection with the former, which may perhaps return with a renewal of the old conditions. Many groups of organisms are incapable of preservation in the fossil state, except under the rarest conditions—conditions which occur so seldom, and so widely separated in space and time, as to render hopeless any attempt to reconstruct a continuous story from them.

The very circumstances under which organisms are preserved in the rocks offer another obstacle to the determination of phyletic series. On examining large collections of fossils from several successive horizons, we find that the majority of the species and even of the genera are confined to one or two formations, and that each succeeding fauna is recruited partly by migrations from other regions and partly by the rapid expansion of comparatively few adaptive and plastic types, while most of the forms which were especially well fitted for the older conditions die out under the new. The collections are, of course, largely made up from the abundant and dominant species of each horizon, which frequently are not the ancestors of those which will be dominant in the succeeding one. The sudden appearance, as it so often seems to be, of a fully differentiated group is sometimes due to that cause, sometimes to a migration from some other region. Even in phyletic series which are well-nigh complete there is a tendency for each successive genus to undergo similar cycles of specific variation, and this adds to the confusion, the very completeness of the record increasing the difficulty of its interpretation.

(2) a second drawback to the paleontological method of inquiry lies in the incomplete preservation of those organisms which are fossilized. Of plants we find, for the most part, only scattered leaves, rarely the reproductive organs, stems or roots, and often the proper association of the various parts requires the strenuous labor of years. Of animals, except under exceedingly rare circumstances, only the hard parts, teeth, bones, shells and the like, are preserved, and in the case of vertebrates how seldom is even the skeleton completely recovered! As in plants, the association of the various parts of a single skeleton may require the long continued and laborious efforts of many workers. Extraordinary blunders have sometimes been committed in this work. In the remarkable genus *Chalicotherium* the skull was at first referred to one mammalian order and the feet to another, and Forsyth-Major's suggestion that they all belonged together was received with incredulity. Of the even more curious *Agriochœrus* the head was ascribed to one order, the fore-leg to a second and the hind-foot to a third.

The utterly false notion, which nothing seems able to eradicate, that the paleontologist can readily restore an extinct type from a single bone or tooth, ought to receive its quietus from such examples, though of course it will not. It is equivalent to saying that we have nothing to learn from the fossils, and that all possible types of structure are exemplified in the living world.

On account of this incompleteness of

preservation we cannot learn much that we wish to know of the structure of extinct organisms. The nervous, vascular, muscular and alimentary systems are entirely lost and can be inferred only from indirect and often insufficient evidence. Were the pearly nautilus extinct, our notions of the anatomy of the tetrabranchiate cephalopods would be very much astray, and in the cases of several groups of fossils we are quite unable to interpret the structure from what remains.

(3) A third difficulty in the way of a truly morphological paleontology consists in the uncertainties of geological correlation, by which the relative age of formations in widely separated areas and different continents is to be determined. It may and often does make a vital difference in the construction of a phylogeny, whether a given set of rocks in North America is older or younger than one in Europe, with which it is correlated. The principles according to which such correlation is to be made are still somewhat indeterminate, and not a few geologists maintain that the problem is an insoluble one. On the other hand, it is essential to the paleontologist that it should be solved, and already a very encouraging beginning has been made.

(4) In the fourth place the apparent order of succession of organisms in the stratified rocks must not be too implicitly and uncritically accepted. Animals and plants diffuse themselves as widely as possible until stopped by some impassable barrier. During the long ages of the world's history these migrations have ever been in progress, and they greatly confuse the record when we attempt to read it in terms of evolutionary descent. A species in a newer formation, which appears to be derived from one in an older horizon of the same region, may, as a matter of fact, have had an entirely different ancestry and have migrated half around the globe to the place where it occurs. To make these distinctions theoretically is easy; to apply them very difficult.

(5) Lastly should be mentioned a practical drawback to the paleontological method, namely, its costliness. The naturalist may find much to do in other departments at small expense, which will be a source of infinite pleasure to himself and of great value to science. Every field and wood, every pond and stream, and above all the sea, offer boundless stores of material. Even the side of paleontology which bears upon stratigraphy and historical geology may be taken up to great advantage by the private worker who happens to live in a favorable locality. With paleontology as a branch of morphology, however, the case is unhappily very different. Here great collections brought together without much regard to cost, skilled workers to prepare the specimens, and great buildings in which to house them are indispensable. Distant regions must be examined and the whole world ransacked for material. Many problems connected with the North American fauna must await their explanation until Asia can be thoroughly explored, while Africa and South America have already shown what a complete geological knowledge of those continents may be expected to teach. In this country the arid parts of the West have yielded a marvelous store of wonderfully preserved fossils, but great sums have been expended in gathering them—an opportunity which falls to the lot of but few. It is to be hoped that the multiplication of museums may ere long put within the reach of all biological students something of these great stores of wealth.

It might well seem that all these limitations and drawbacks would necessarily disqualify paleontology as a morphological subject from being of the smallest real importance, but such a conclusion would be highly erroneous. Several of the limitations are but partial, not applying to par-

ticular cases, while others are difficulties that further investigation may hope to remove, not insurmountable obstacles. Every year new forms are discovered and better material of known forms. Though the White River Bad Lands have for more than half a century been classic collecting ground, hardly a season passes that several new genera are not registered from there, and, better still, types before known only from fragments are gradually made more and more complete. From the middle Eocene to the lower Miocene there is in the West an almost unbroken transition which is bringing forth a truly magnificent series of evolutionary stages.

While paleontology, as we have seen, does not profess to give an unbroken life history of the earth, yet it has certain preeminent advantages which neither comparative anatomy nor embryology possesses, and which fit it to form an invaluable supplement to those other methods of morphological investigation.

(1) In the first place, it gives us in many cases actual phyletic series in their true order of succession in time. In many groups of animals we have already recovered phyletic series so full, so complete, that no observer can hesitate to accept them as representing actually or very nearly the successive steps of evolutionary change in the order in which they occurred. Little confidence may, perhaps, be placed in these phyla by those who have not made a special study of them, and it may be imagined that fuller knowledge will require them to be completely changed. But when we find such a series as that of the horses, leading back by almost imperceptible gradations from the great monodactyl living forms to their little five-toed progenitors in the far distant Eocene times, doubt becomes well-nigh impossible. A limit of error is placed by the stratigraphical order, the geological and morphological successions coinciding beautifully. Whatever changes in the details of such a series may be needed, a radical reconstruction of it is not in the least likely to be called for. Few observers, if any, would now uphold the arrangement of the equine phylum proposed by Kowalevsky, namely, *Palæotherium*, *Anchitherium*, *Hipparion*, *Equus*; and yet it is surprising to see how the general character of this series, and the deductions as to the manner of evolution which may be drawn from it, agree with those made on the basis of the equine series as we now have it. Kowalevsky's mistake merely consisted in putting certain members of the side branches into the main line of descent, and that similar errors have been made in accepted phylogenies is not at all unlikely. The correction of such errors will, however, change the general result but little, and we may appeal with considerable confidence to the conclusions which legitimately follow from a study of these phylogenies.

Fortunately, the well-defined phyletic series which have already been made out occur in very widely separated animal groups—mammals, reptiles, cephalopods, brachiopods, echinoderms, etc.—so that the points in which they agree are apt to prove of general application and validity. The cephalopods are particularly valuable in this connection, because in them the embryonic and young stages of the shell are preserved in the adult, and thus conclusions have a distinct support from embryological considerations. To recur to the linguistic analogy, we have here at least fragments, and sometimes very extensive ones, of the various literatures which register the changes of language, and in the original documents which bear evidence of their dates and succession, and which, however incomplete, have not been falsified by forgeries and late interpolations. In this way we may establish unequivocally some, at least, of the animal pedigrees, which it is

one of the great objects of morphology to construct, and thus to correct the results obtained by the other methods of inquiry.

Paleontology further enables us accurately to discriminate between resemblances which are due to genetic affinity and those which result from parallelism or convergence.

To illustrate: On grounds of comparative anatomy, Flower classified the land Carnivora in three sections: the Cynoidea, or dogs; the Arctoidea, containing the bears, raccoons and mustelines; and the Aeluroidea, including the civets, hyenas and cats. This classification has found wide favor and very general acceptance, but paleontology proves it to be untenable. The extinct phyla show that the dogs and bears are very closely akin, as are the mustelines, civets and hyenas, while the cats occupy a very isolated position and are not nearly allied to any of the other families. The anatomical characters which suggested Flower's system are, in part, examples of convergence, and in part, due to the retention of primitive characters in some groups and their loss in others.

Again, reasoning from embryological data, Röse and others have propounded the theory that the complex, multicuspidate, mammalian tooth has been formed by the coalescence of many simple teeth. The phyletic series enable us to follow the evolution of these teeth step by step, and demonstrate the incorrectness of the 'concrescence theory.' In fact, the great lesson which the study of the phyla continually brings home to the observer is that trustworthy results are to be obtained only by the laborious and minute tracing of the changes through every step of the way. Fragmentary series are not to be depended upon, and the wider the gaps between their members the more uncertain is their connection.

(2) The reconstruction of pedigrees, the solving of homologies, the determination of relationships, and the establishing of classification upon a sound and natural basis, important as these are, are yet only a part of the great task which morphology has set before itself. We wish to penetrate more deeply into the mystery of nature and learn how and why these changes have occured; or, in other words, to discover the manner in which, and the efficient causes by which, development is effected. On these subjects there is, as yet, wide divergence of view among morphologists. The postulates and assumptions upon which morphological discussions are founded are, in great measure, incapable of proof, and appeal with very different degrees of force to different minds. Modes of development which appear axiomatic to one observer are by another regarded as absurd. All are agreed that there are limits to the possibilities of change; no one attempts to derive a butterfly from a beetle, or a horse from a cow; but just how and where these limits should be drawn it is at present impossible to say. It is this uncertainty which refers the question to the individual judgment and leaves the way open for such radical differences of opinion.

To the solution of these problems of evolutionary modes paleontology offers most valuable assistance, drawn from the study of actual phyla. It might seem that this was merely arguing in a circle, because the construction of phylogenetic series involves certain presuppositions as to what changes are and what are not possible, and we then proceed to prove the presuppositions by the phyla thus constructed. But the cautious, step-by-step method, guarded by the order of appearance in time, offers a way of escape, and enables us to construct phyla in harmonious structural and stratigraphical succession, which must very nearly represent the actual stages of change. Only a beginning has been made in this work, but the results drawn from an examination of

widely separated phyla, such as mammals, gasteropods and cephalopods, are so consistent and harmonious as to be full of promise for the future.

Limitations of time and space forbid an attempt to fully consider here all the deductions which have been suggested and rendered more or less probable by this method, but one or two principles which stand out with especial clearness may be mentioned.

(*a*) Evolution is ordinarily a continuous process of change by means of small gradations. The continuous character of a phylum is apt to be proportional to the relative abundance of its representatives in the strata, which is equivalent to saying that well-known series are continuous, while apparently discontinuous series are imperfectly known. This does not imply that the rate of change was always uniform—it probably was not—or that a sudden alteration of conditions may not bring about discontinuity, or *per saltum* development. It means that the usual and normal mode of advance is by continuity of change.

(*b*) Development is, in most instances, direct and unswerving. The rise of new forms, and the decadence and degeneration of old ones, are not ordinarily by zigzag and meandering paths, but by relatively straight ones; and though, of course, a path once taken may be diverged from, yet in such a case it is not regained. This applies particularly to the organism as a whole; in minor details more latitude is permissible. The evidence is not yet sufficient to show just how widely applicable this principle is.

(*c*) Parallelism and convergence of development are much more general and important modes of evolution than is commonly supposed. By parallelism is meant the independent acquisition of similar structure in forms which are themselves nearly related, and by convergence such acquisition in forms which are not closely related, and thus in one or more respects come to be more nearly alike than were their ancestors. While some observers have tacitly or explicitly denied the reality of these processes, most authorities have been compelled to admit them. What paleontology has done, and is doing, is to show the universality of these modes of development, and to point them out in directions where they had not been suspected. To give a few examples: The crescentic, or selenodont, molar has been separately acquired by no less than three groups of artiodactyls, and probably others as well. The spout-shaped odontoid process of the axis has independently developed in the horses, the tapirs, and in three artiodactyl series. The true ruminants (Pecora) of the present day are, among other characteristics, distinguished from the remaining artiodactyls by the hollow tympanic bullæ, which in the pigs, tragulines and camels are filled with cancelli, or spongy bone. In Oligocene times only the camels had acquired the cancelli; the other groups, though already differentiated as such, still had hollow and inflated tympanics. Lists of such parallelisms in single characters might be multiplied almost indefinitely, but they also occur in whole groups of structures. The camels have in teeth, skull, vertebræ and limbs many points of resemblance to the true ruminants, which demonstrably are not due to inheritance from a common ancestor. The two great series of ungulates, the artiodactyls and perissodactyls, which are usually grouped together as the Ungulata *par excellence*, are examples of parallel development on a grand scale, their many resemblances being for the most part independently acquired. The flesh eaters known as Carnivora include at least two, and probably three lines, which have been separately given off from the primitive flesh eaters, or creodonts.

Such a mode of development greatly increases the difficulty of determining phy-

logenies, which would be very much easier could every notable resemblance at once be accepted as proof of relationship. It often renders impossible the proper classification of some isolated genus which seems to have several incompatible affinities. It emphasizes the necessity of founding schemes of classification upon the totality of structure, and of determining the nature of characteristics, whether they are primitive or acquired, divergent, parallel or convergent, before attempting to assign them their proper taxonomic value.

We may find a practical identity in teeth, skull or feet as the outcome of these processes, but as yet no case is known where all these structures have become alike through the operation of either parallel or convergent development. Among the invertebrates the case is different. Hyatt has shown that the degenerate, straight-shelled, ammonoid genus *Baculites* is a polyphyletic group, and derived from several distinct stocks, both European and American. Würtenberger points out that the so-called *Ammonites mutabilis* is not a true species, but a composite group, made up by the convergence of several distinct lines to a common term. This case is peculiarly significant, because it would hardly have been detected had not the embryonic and young stages of the shells been preserved.

It seems the most obvious of commonplaces to say that numerous and close resemblances of structure are *prima facie* evidences of relationship. Yet the statement is true, even though the resemblances have been independently acquired, because parallelism is a more frequently observed phenomenon than convergence, and because the more nearly related any two organisms are, the more likely are they to undergo similar modifications.

All this brings us back to the thesis so frequently insisted upon already, that the only safe and trustworthy method of constructing phylogenies is by tracing the development, step by step, through all its gradations; and until this is done the classification of any group can be but tentative and provisional, that is, if we intend classification to express relationship.

No department of biological science is at present the scene of such vigorous controversy as that which deals with the factors of evolution, the causes which determine the development of new forms, and the problems of heredity which are inseparably connected with them. Paleontological evidence will prove to be of much importance in this connection also, but it cannot well have more than a corroborative value. Though the examination of long and complete phyla brings to light much that is suggestive concerning the factors which have brought these changes to pass, and any rational theory must embrace and explain these facts, yet the deciding weight must probably come through the physiological and experimental method. Time fails to deal with such far-reaching questions here, and yet it may be well to call attention to the necessity of avoiding a dogmatic and intolerant attitude, and to deprecate any premature attempt to exclude this or that class of factors from consideration. In most of the recent writings upon the efficient causes of evolution you will find expressed or implied the feeling that these matters are not so simple and intelligible as we once supposed, and that we are yet only upon the threshold of their solution. The study of paleontology will not tend to dispel this feeling of mystery.

Another department of biological science in which paleontology has proved of great value, and will become more and more so in the future, is that which deals with the geographical distribution and migrations of organisms. Though not a branch of morphology, this subject has a very significant bearing upon that science, and cannot be

ignored in any comprehensive theory of evolution. This, again, is too large a field to enter upon at the close of a lecture. It must suffice, therefore, to hint at the many cases in the existing distribution of animals, which seem so puzzling and capricious, and which are so readily explained by a study of the past. That the nearest allies of the South American llamas should be the camels of the Old World seems unaccountable, until we learn that North America was the original home of the entire tribe. The occurrence of the tapirs in South America and in the Malay peninsula becomes intelligible enough, when we learn that this genus is of very high antiquity, and was formerly represented in every part of the northern hemisphere.

The more fully the past is recovered, the more completely the former land connections of the various continents are made out, the more comprehensible do the seeming anomalies of the present order of things become—a proposition which applies to more than problems of geographical distribution.

The foregoing consideration of paleontology as a branch of morphological science is necessarily brief and very inadequate, but it will suffice, I trust, to show that its claims upon the attention of morphologists should not be ignored, and that it is admirably fitted to throw light upon many obscure problems. In conclusion, let me point out that final and lasting results are not to be gained by an exclusive adherence to any method of morphological inquiry, but by a combination of all of them. Each is able to supplement the others, and it is folly to reject such aid. Already most encouraging results have followed from this combined method of work, and it is devoutly to be wished that its scope may be more and more extended. As an example may be cited the recent investigations upon the mammalian dentition. From paleontological phyla we have learned to distinguish the homologies of the cusps, and the way in which a complex tooth is gradually formed from a simple one. Embryology, on the other hand, has shown the relations of the successive dentitions to one another in a fashion that paleontology could by no possibility accomplish unaided. As another example may be mentioned Wincza's discovery of a bony clavicle in the embryo of the sheep, which was soon followed by the still more unexpected one of vestigial bony clavicles in certain extinct artiodactyls, confirming and explaining the first. Embryology has taught us that the large element in the carpus of the Carnivora known as the scapholunar was formed by the coalescence of three separate bones—the scaphoid, lunar and centrale. Later the fossils were unearthed, which showed that the embryonic and transitory condition of the modern forms was the permanent and adult structure of the primitive Eocene flesh-eaters.

The more the combined method is employed the more fruitful does it appear. Nor should the combination be restricted to the technically morphological subjects. Experimental embryology has already won some notable triumphs, and that is a physiological quite as much as a morphological province.

In the ever-increasing complexity of modern civilization a more and more important rôle is played by systematic coöperation, specialists combining for joint work which neither could accomplish alone. Is it Utopian to wish that some such organized scheme of attack upon biological problems shall be devised, when, instead of every man doing merely that which is right in his own eyes, we shall combine in a definite, orderly way to investigate a given topic in all its bearings? It may well be doubted whether any naturalist, however great his genius, will ever again be able

to take such an exhaustive survey of biological data as Darwin did in his time. The enormous mass of accumulated facts already far transcends the power of any one mind to grasp, and it would seem that organized cooperation is the only method of dealing with such vast accumulations. When that time arrives, the paleontologist will be able to render even more conspicuously valuable services that he has done in the past.

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ON PHOLADIDEA PENITA AND ITS METHOD OF BORING.

The Piddock of the northwestern coast, Pholadidea penita, is found in its curved conical burrow in the rocks near the tide marks. These rocks, so far as the writer's observation goes, consist of soft limestone or sandstone of varying hardness, the animal choosing the softer portions for its home. How the Piddock accomplishes the task of burrowing into the even moderately hard sandstone is a question upon which little light is thrown by an examination of the mature, or as I shall call it, the resting form, which is characterized by the complete absence of its foot muscles and an almost complete fusion of the mantle lobes along their ventral margin, leaving an opening hardly 2 mm. long. The inference is that Pholadidea penita is a degenerate form, as is the oyster. Further facts, however, will show that this degeneracy does not occur till late in life, when its burrow, the home of its old age, is completed.

The shell of the animal during its period of diligence, like that of other Piddocks, gapes widely in front. Through the upper portion of this gape protrudes a thick fold of the mantle which overlaps the antero-dorsal margin of each valve and secretes a layer of calcareous matter on the outside of the shell. The gape is much wider below and through it protrudes a strong cylindrical muscular foot, the muscles of which are attached at a point of vantage supplied by a curved process on the inside of each valve. The mechanical result of this ar-

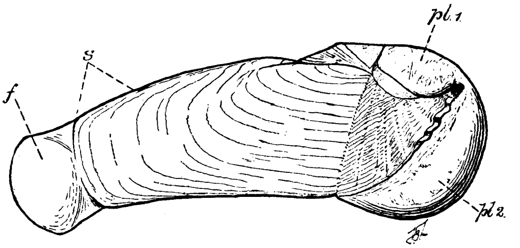

Fig. I. Left side of resting form, specimen 9 cm. long.

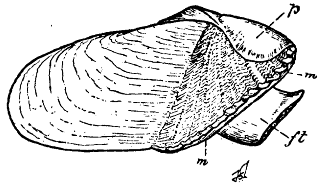

Fig. II. Left side of working form, specimen 6 cm. long.

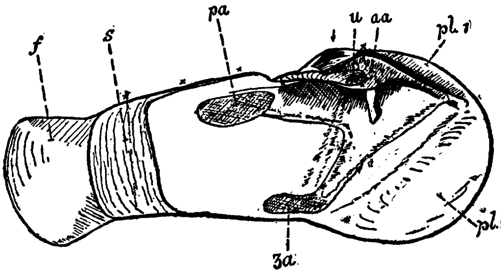

Fig. III. Inside of left valve showing hinge mechanism and muscle markings, specimen 9 cm. long; Siphon retracted in all. aa. Anterior adductor muscle mark; the arrow point indicates its posterior limit. 3a. Third adductor muscle mark at angle of pallial sinus. f. Cuticular flap. ft. Foot. m. Thick antero-ventral edge of mantle surrounding foot. p. Pad formed by antero-dorsal mantle folds. pa. Posterior adductor muscle mark. pl. 1. Plate secreted by antero-dorsal mantle fold, of that side. pl. 2. Plate secreted by m. in Fig. II. S. Additional extent of shell added at the same time with cuticular flap. u. Umbo. The leaders end in patch of abrasion, the point where the valves articulate. The small crosses indicate attachment of hinge cuticle.